AN ECOLOGICAL SNAPSHOT OF THE EARLY PLEISTOCENE AT KOKISELEI, KENYA

by

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STATEMENT OF THESIS APPROVAL

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ABSTRACT

Fauna from hominin-bearing Pliocene and Pleistocene sites in the Omo-Turkana Basin have long been valuable in assessing how the climate of East Africa over the past 5 Ma has changed. Stable C and O isotope ratios in the enamel of fossil herbivores at a *Paranthropus boisei*-bearing Pleistocene archaeological site on the west side of Lake Turkana give insight on vegetation coverage and moisture conditions for this area between 1.87 and 1.80 Ma; samples were from a faunal assemblage associated with excavations at two sites at Kokiselei. Average $\delta^{13}C$ enamel values of -1.6 ± 3.6‰ (n=80) indicate a C_4-dominated landscape. Equids, suids, hippopotamids, and most bovids have C_4-dominated diets; tragelaphines have mixed C_3- C_4 diets; *Giraffa* and *Deinotherium* have a C_3-dominated diet. Average $\delta^{18}O$ values of +0.2 ± 1.7‰ indicate the presence of water relatively less enriched in ^{18}O than modern Turkana Basin waters that have been measured. Low $\delta^{18}O$ values in evaporation-sensitive taxa such as *Giraffa* indicate less aridity than modern Turkana grassland and shrubland. Overall results suggest that during the early Pleistocene, *P. boisei* inhabited dominantly open wooded grassland that experienced a significantly different moisture regime from that of the present day.

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INTRODUCTION

Understanding how landscapes and ecology have changed over geologic time is essential to unraveling the story of human evolution (Laporte and Zihlman, 1983; Potts, 1998; Kingston, 2007; Levin et al., 2008). While hominin evolution was once seen as linear, decades of paleoanthropologic research reveal a more complex series of adaptive radiations resulting from changes in their environment, including appearance of megadontic hominins on the landscape during the Plio-Pleistocene (Kay, 1985; Foley, 2003). Fossil remains of *Paranthropus boisei,* a member of the megadontic hominin lineage, have been found in Plio-Pleistocene deposits at Omo and Konso in Ethiopia, West Turkana, Koobi Fora, and Chesowanja in Kenya, Peninj, Olduvai, and Laetoli in Tanzania, and Malema in Malawi. *P. boisei* is considered to have occupied the East African landscape from 2.3 Ma to at least 1.4 Ma, the age of the geologically youngest remains from Konso in Ethiopia (Wood and Constantino, 2007). Varying environments have been suggested for *P. boisei*, from closed, wet habitats (Shipman and Harris, 1988) to a more open one with edaphic grasslands (Reed, 1997). Also on the scene at the same time in the Omo Turkana Basin were other hominins, including *Homo rudolfensis, H. habilis, and H. ergaster* (Wood and Leakey, 2011). Hominins preceding these in the area were *Kenyanthropus platyops*, *Australopithecus afarensis*, and *Au. anamensis*.

As a period in earth's history during which members of both *Paranthropus* and *Homo* coexisted (Kingston, 2007), the early Pleistocene offers valuable insight into the evolution and co-evolution of our hominin ancestors. Climate during the Plio-Pleistocene shows an overall drift toward increased grassland and the spread of open versus closed vegetation coverage; marine foraminifera and pollen records show that this long-term

trend was accompanied by increased variability (Potts, 1998; DeMenocal, 2004; Levin et al., 2011). Many studies of climate in East Africa focus on the mode and tempo of these changes, but here isotope data from a single faunal assemblage are used to examine paleoclimate in the early Pleistocene. Paleosol carbonates show a grassy woodlands signal until 2 Ma, followed by a shift towards an open grassland after the Plio-Pleistocene transition (Cerling et al., 1988; Sikes, 1994; Sikes et al., 1999; Wynn, 2000; Levin et al., 2004; Quade et al., 2004). Enamel isotope studies of fossil fauna from the region during the same period show C_4-dominated diets among proboscideans and equids since 7 Ma, until modern elephants switched back to browsing (Cerling et al., 1999; Zazzo et al., 2000; Kingston, 2007)

Ecological changes happen on many temporal and geographic scales. Research in East Africa has now established regional and millennial trends, but to truly understand the variety of environments in which hominins moved, a more detailed record is essential. In this thesis, I help fill in some of those details, adding a puzzle piece to the mosaic of Plio-Pleistocene climate and fleshing out interbasinal climate within the Omo-Turkana Basin.

In this study, stable isotopes are used to provide a composite portrait of life in East Africa during the early Pleistocene; this uses $\delta^{13}C$ and $\delta^{18}O$ measurements taken from fossil enamel excavated at Kokiselei in Kenya (Fig. 1). The stable isotope composition of enamel has been used in paleoenvironmental studies to examine diet, expansion of C_4 grasses, and aridity (DeNiro and Epstein, 1978; Cerling et al., 1997; Levin et al., 2006). This study attempts to reconstruct vegetation cover and moisture conditions for a 700 thousand year slice of geologic time in the Turkana Basin.

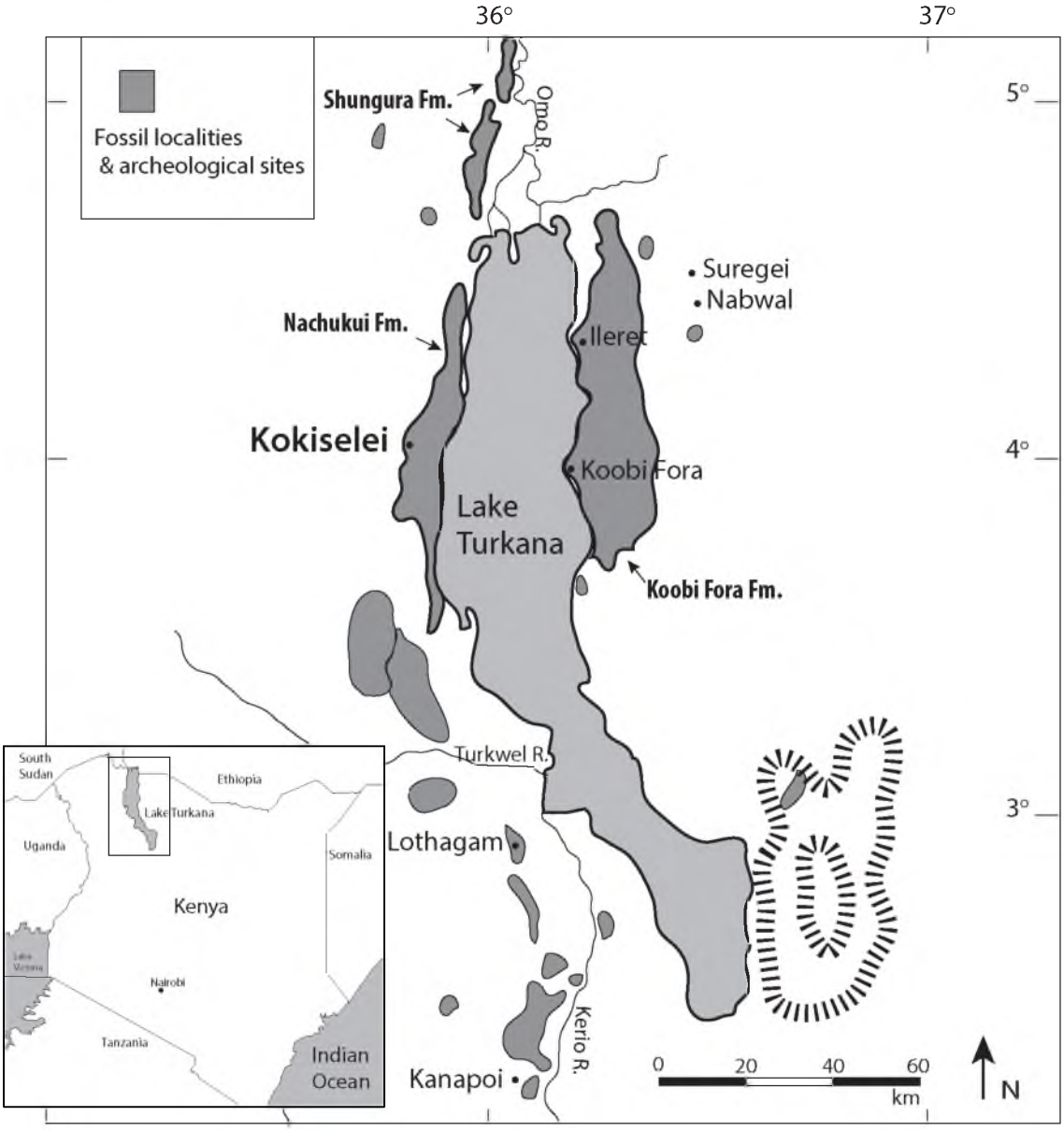

Figure 1 Turkana Basin showing location of formations and fossil sites. Sites other than Kokiselei represent locations for modern enamel samples.

BACKGROUND

Kokiselei and Geological Setting

Lake Turkana occupies the Omo-Turkana Basin, a depositional environment since 4.2 Ma (Brown and Feibel, 1991). The Omo-Turkana Basin is in the eastern branch of the East African rift-system, which developed in the Paleogene (Baker et al., 1972; Pik et al., 2008; Roberts et al., 2012). Currently alkaline and a closed-basin lake, Turkana's main fluvial input is the Omo River from the north, fed by rains from the Ethiopian highlands (Yuretich and Cerling, 1983). Rift-related volcanism formed many layers of volcanic ash in the Turkana Basin, which are K/Ar and $^{40}Ar/^{39}Ar$ dated and serve as tephrochronology for the depositional facies found within the stratigraphy (Feibel et al., 1989). During the Miocene, there is evidence of a fluvial corridor to the Indian Ocean, an extensive fluvial system, and possibly the presence of broad floodplain development. Lonyumun Lake, the first of the Plio-Pleistocene lakes, formed 4.1 Ma and was the largest lake to fill Turkana Basin (Feibel, 1988). Sediment influx into the lake was larger than basin subsidence, and a fluvial floodplain replaced Lake Lonyumun, called the Moiti Floodplain, at 3.97 Ma. During this period, the Omo River was a large meandering river (Ward et al., 1999). The next lake to occupy the basin was called Lokochot Lake at 3.4 Ma; following this, the Tulu Bor Member included two small lakes, the Waru and Kokiselei Lakes. Volcanic activity associated with Mount Kulal developed ~2.5 Ma and plugged the Omo, leading to the formation of the Lorenyang Lake ~2.0 Ma, present on the landscape during the deposition of Kokiselei 1 and 2 (Levin et al., 2011). Stratigraphy

suggest this was a period of complex landscape evolution, including lakes, deltas, and fluvial systems (Brown and Feibel, 1991; Feibel, 2011).

Kokiselei is an archaeological complex on the western side of Lake Turkana, excavated by the West Turkana Archaeological Project (WTAP), a collaboration between the National Museums of Kenya and the *Mission Prehistorique au Kenya*. The Kokiselei complex (KS) consists of ten sites; it is contained in the upper Kaitio Member of the Nachukui Formation, part of the Omo Group (Brown and Feibel, 1991; Lepre et al., 2011) (Fig. 2). The Kaito Member is between the KBS and Morutot Tuffs, dated at 1.87 and 1.61 Ma, respectively (McDougall and Brown, 2006). Teeth analyzed for isotopes in this study belong to Kokiselei 1 (KS1) and Kokiselei 2 (KS2), the two stratigraphically oldest sites, but Morutot is not present at Kokiselei and so age is not well constrained. Correlations with regional geologic sections indicate that Kokiselei is between 1.87 and 1.80 Ma in age, assuming a constant rate of sedimentation. Five square meters have been excavated from Kokiselei, but exact stratigraphic providence of KS1 and KS2 has yet to be specified. Fossils and artifacts found were scattered within a 28 cm vertical range (Kibunjia et al., 1992). Oldowan tools as well as *P. boisei* teeth are found at KS1, with Acheulean lithics stratigraphically older, in KS4 (Roche et al., 2003). Kokiselei lies within silty claystone deposited between a paleo-lakeshore and alluvial plains to the west. Nearby strata consists of a conglomeratic sandstone with pebble and cobble sized clasts of volcanics and mollusk-packed sandstone, interpreted as high-energy shoreline deposits (Kibunjia et al., 1992).

Chemical Composition of Bioapatite and Diagenesis

Enamel is composed of 96% mineral (Elliott, 2002), a bioapatite called hydroxylapatite. In bioapatite, carbonate (CO_3^{2-}) can substitute into the phosphate

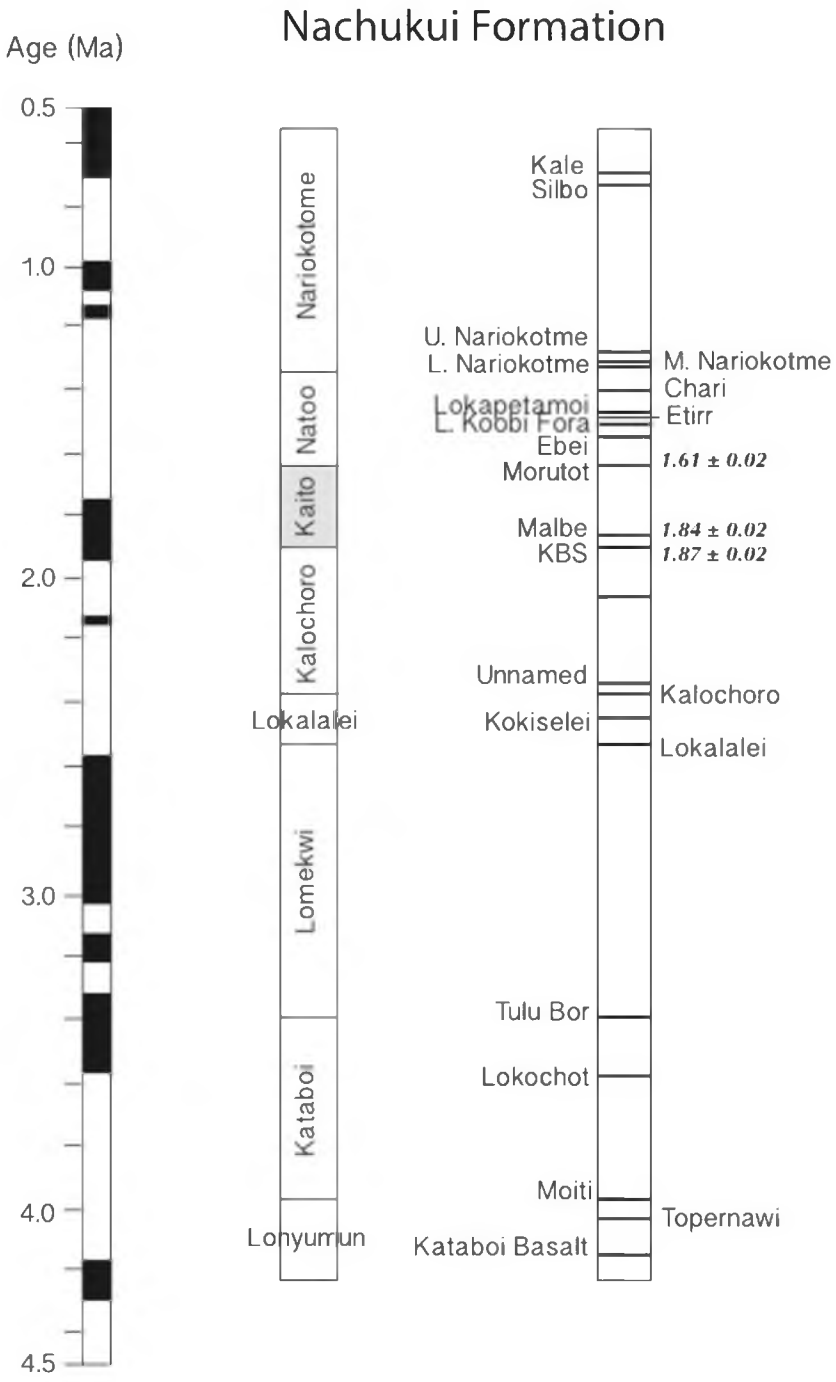

Figure 2 Paleomagnetic stratigraphy, Nachukui Formation and members contained, and tuff markers found within. Stratigraphy is modeled after Levin et al. (2011), based on Brown et al. (2006), Brown and Feibel (1991), Cande and Kent (1995), McDougall and Brown (2006, 2008). Tuff markers are named in the third column, but not all are found within the Nachukui Formation.

(PO_4^{3-}) or hydroxyl (OH^-) position in the $Ca_{10}(PO_4)_6(OH)_2$ molecule (Hillson, 2005). Substituted carbonate is derived from blood bicarbonate; this CO_3^{2-} is the source of the $\delta^{13}C$ and $\delta^{18}O$ in bioapatite (Lee Thorp, 2002). Stable isotope ratios are reported here relative to the standard Vienna Pee Dee Belemnite (VPDB), where

$$\delta^{13}C\ (‰) = [(^{13}C/^{12}C)_{sample}/(^{13}C/^{12}C)_{standard} - 1] \times 1000$$

and

$$\delta^{18}O\ (‰) = [(^{18}O/^{16}O)_{sample}/(^{18}O/^{16}O)_{standard} - 1] \times 1000.$$

X-ray diffraction of enamel has established that apatite crystals grow in the orientation of enamel rods, which extend from the enamel surface to the enamel-dentine junction (EDJ). Their diameter ranges from 4-7μm (Elliott, 2002). Their integrity within the fossil record is dependent on their large crystal size, over 1000 Å larger than apatite crystals in bone, in the case of hippo enamel (Elliott, 2002). Being more crystalline and more dense, enamel is less subject to recrystallization and yields higher concentrations of carbonate (Lee-Thorp and van der Merwe, 1991; Koch et al., 1997; Ayliffe et al., 2004). X-ray diffraction comparing enamel to dentine, cementum, and bone show enamel to be unaffected by digenetic recrystallization, at least for fossil enamel dating up to 3.44 Ma old (Ayliffe et al., 1994; Kohn and Cerling, 2002).

Carbon Isotopes

Carbon isotope ratios ($^{13}C/^{12}C$) can be used in enamel, tissue, and breath studies to establish the diet of the animal (DeNiro and Epstein, 1978; Cerling and Harris, 1999a; Passey et al., 2005). This is due to the distinctive $\delta^{13}C$ signal of C_3 and C_4 plants, which have differing photosynthetic pathways for fixing CO_2 (Farquhar et al., 1989). C_3 plants mainly consist of trees, shrubs, herbs and forbs, and cool growing season grasses. C_4 plants include sedges, and some shrubs, but mainly warm growing season grasses. Trees

and shrubs in East Africa have C_3 pathways while most grasses have C_4 pathways, aside from high altitude grasses (>3000m) (Tieszen et al., 1979; Young and Young, 1983).

Two main processes govern carbon isotope fractionation in plants, diffusion of CO_2 through stomata and discrimination against ^{13}C by the carboxylating enzymes, RuBisCO in C_3 plants and phospoenolpyruvate carboxylase in C_4 (Farquhar et al., 1989). Most C_3 vegetation has $\delta^{13}C$ values that range from around -30‰ to -22‰ whereas $\delta^{13}C$ values of the majority of C_4 plants range from -14‰ to -10‰; nominal average values for C_3 and C_4 plants are often taken to be -26.5‰ and -12.5‰, respectively (Lee-Thorp and van der Merwe, 1991). Three main classifications of vegetation coverage at low elevations in Equatorial Africa can be identified by their average $\delta^{13}C$ values. Closed canopy vegetation is depleted in ^{13}C, with $\delta^{13}C$ values <-30‰ (van der Merwe and Medina, 1991; Cerling and Harris, 1999b; Cerling et al., 2004). Forest and bushland in more open environments are more enriched in ^{13}C, with an average $\delta^{13}C$ value ~ -27‰ (Cerling and Harris, 1999b). Water stress can alter these values, enriching C_3 plants in ^{13}C. As stomata close to reduce water loss, the diffusion rate decreases, which results in less discrimination against ^{13}C (Farquhar et al., 1989; Ehleringer et al., 1993).

$\delta^{13}C$ values in plants consumed by ungulate mammals undergo an isotope enrichment process of 14.1 ± 0.5‰. This enrichment ε^* is expressed as

$$\varepsilon^* = [(\delta_A+1000)/(\delta_B+1000)-1] \times 1000$$

where ε^* indicates that the two systems are not at equilibrium (Cerling and Harris, 1999b). Enrichment of $\delta^{13}C$ values in enamel occurs upon the metabolism of the diet and during amelogenesis of enamel. Methanogenesis in the gut produces the following reaction: $2CH_2O = CH_4 + CO_2$ in which the methane $\delta^{13}C$ value is depleted and the carbon dioxide $\delta^{13}C$ value is enriched. There is also enrichment between CO_2 in blood bicarbonate and enamel CO_3^{2-} that is constant for all mammals (Passey et al., 2005).

With an enrichment of 14.1 ± 0.5‰, a C_3 diet would have an average $\delta^{13}C$ value of -13.1‰ and a C_4 diet would have an average $\delta^{13}C$ value of +3.1‰.

Oxygen Isotopes

Oxygen isotope ratios ($^{18}O/^{16}O$) in organic tissue are related to the isotopic composition of environmental waters, including metabolic water (Luz et al., 1984). This makes it possible for oxygen isotopes to be used as an aridity index. ^{18}O enrichment occurs during evaporation, due to kinetic equilibrium effects (Sharp, 2007). Their use in aridity studies is dependent on species falling into two categories, "evaporation sensitive" (ES) and "evaporation insensitive" (EI). In ES species, the $\delta^{18}O$ values of their enamel reflect the aridity of the environment—where increasing $\delta^{18}O$ values reflect increasing aridity. In EI species, these values instead reflect those of local meteoric water (Levin et al., 2006).

This difference between ES and EI species can be explained by where these animals source their water. ES animals tend to restrict their intake of water to their food as with a minor amount derived by directly drinking water. When this is a diet mainly of leaves, the leaves act as miniature lakes in terms of evaporative enrichment of ^{18}O, meaning that the animal's $\delta^{18}O$ signal tracks aridity. EI species generally live in or near water, and drink directly from the source. Proximity to water means that their intake is not restricted to only evaporated sources, meaning their $\delta^{18}O$ signal tracks LMW (Levin et al., 2006), which may or may not be evaporated, or which may vary depending on the season.

Levin (2006) developed a quantitative method to evaluate water deficit (WD) using isotopic enrichment between ES and EI $\delta^{18}O$ enamel values ($\varepsilon_{ES\text{-}EI}$). Sample size for Kokiselei is small, so the calculations have not been undertaken.

MATERIALS AND METHODS

Samples

Fossil enamel samples were taken from an existing collection held at the National Museums of Kenya. The teeth belonged to various large ungulates, including proboscidea, and rodents (porcupines and cane rats) found at Kokiselei, Kenya that were collected by Jean-Philippe Brugal of WTAP. Ninety-eight powdered enamel samples from no more than 96 individuals were brought back to the University of Utah for stable isotope analysis. Enamel was removed from the teeth using a Dremel powered diamond bit, yielding 2-9 mg of powder. To avoid contamination, the surface was first cleaned using a separate bit; dentine, cementum, and matrix were avoided.

Modern enamel isotope data from the Turkana Basin is used as a comparative tool. Fauna includes elephants and various ungulates. Sampled areas include Ileret, Kanapoi, Lothagam, Nabwal, Suregei, Koobi Fora, and the Omo River. Data were classified as either Koobi Fora grassland or arid shrubland based on the biome of collection. Samples from Koobi Fora and Ileret fell into both classifications while Nabwal, Suregei, Lothagam, and Kanapoi were classified as arid shrubland. Samples were collected over the past 50 years. Modern $\delta^{13}C$ values were corrected to compensate for bomb-influenced changes to atmospheric $\delta^{13}C$ occurring in the 20th century; hence, the values are recorded as $\delta^{13}C_{1750}$.

Treatment

Samples were treated with 0.1M CH_3COOH for 15 minutes to dissolve secondary carbonates, rinsed with deionized water three times, and then dried at 60˚C for 24 hours. Immediately prior to analysis, they were baked at 200°C for 2 hours to remove any atmospheric carbon dioxide.

Analysis

Samples were analyzed using a 252 MAT Finnigan Duel Inlet mass spectrometer. The powdered enamel was reacted with 100% H_3PO_4 with silver capsules in a collective bath at 90°C. Standards used were an internal Carrara Marble and tooth enamel standards, FGS and FRS. FGS is a fossil gomphothere and FRS is a fossil rhino. All of these standards have been calibrated to NBS-19. *Thryonomys* enamel samples were analyzed in situ using a CO_2 laser, a process fashioned after Passey and Cerling (2006). For laser ablation data, unknowns were corrected against a blank, a CO_2 standard of known value, and a castor beaver standard.

RESULTS AND DISCUSSION

Diet by Taxa

Bovidae

Modern bovid teeth sampled from the Koobi Fora grassland region (hereafter referred to as grassland) include the tribes Alcelaphini, Antilopini, and Hippotragini, identified to species level as *Damaliscus lunatus* (topi), *Gazella granti* (Grant's gazelle), and *Oryx beisa* (beisa or fringe-eared oryx), respectively. Topi have $\delta^{13}C$ values ranging from +1.9‰ to +4.8‰ (average of +3.1 ± 1.0‰, n= 6), the Grant's gazelle has a $\delta^{13}C$ value of -3.8‰ (n=1), and beisa oryx have $\delta^{13}C$ values ranging from -0.7‰ to +3.5‰ (average +1.4 ± 1.8‰, n=5) (Figs. 3-4). The range in values for the oryx can be explained by their tendency to avoid grasslands in the rainy season, and to avoid bushland in the dry season (Kingdon and Pagel, 1997) (Table 1).

Modern bovid teeth from the arid shrubland region (hereafter referred to as shrubland) include the tribes Antilopini, Hippotragini, and Madoquini (formerly included in Neotragini). These have been identified to species level. Antilopini includes *Gazella grantii* (Grant's gazelle) and *Litocranius walleri* (gerenuk), Hippotragini include *O.beisa*, and Madoquini include *Madoqua kirkii* (Kirk's dik-dik). The Grant's Gazelle has a $\delta^{13}C$ value of -11.2‰ (n=1) and the Gerenuk has a $\delta^{13}C$ value of -11.9‰ (n=1). The Beisa oryx enamel values ranged from -1.8‰ to +1.2‰ (average -0.2 ± 1.3‰, n=4). The dik-dik enamel display $\delta^{13}C$ values ranging from -13.3‰ to -6.5‰ (average -10.8 ± 1.8‰, n=16) (Fig. 3-4).

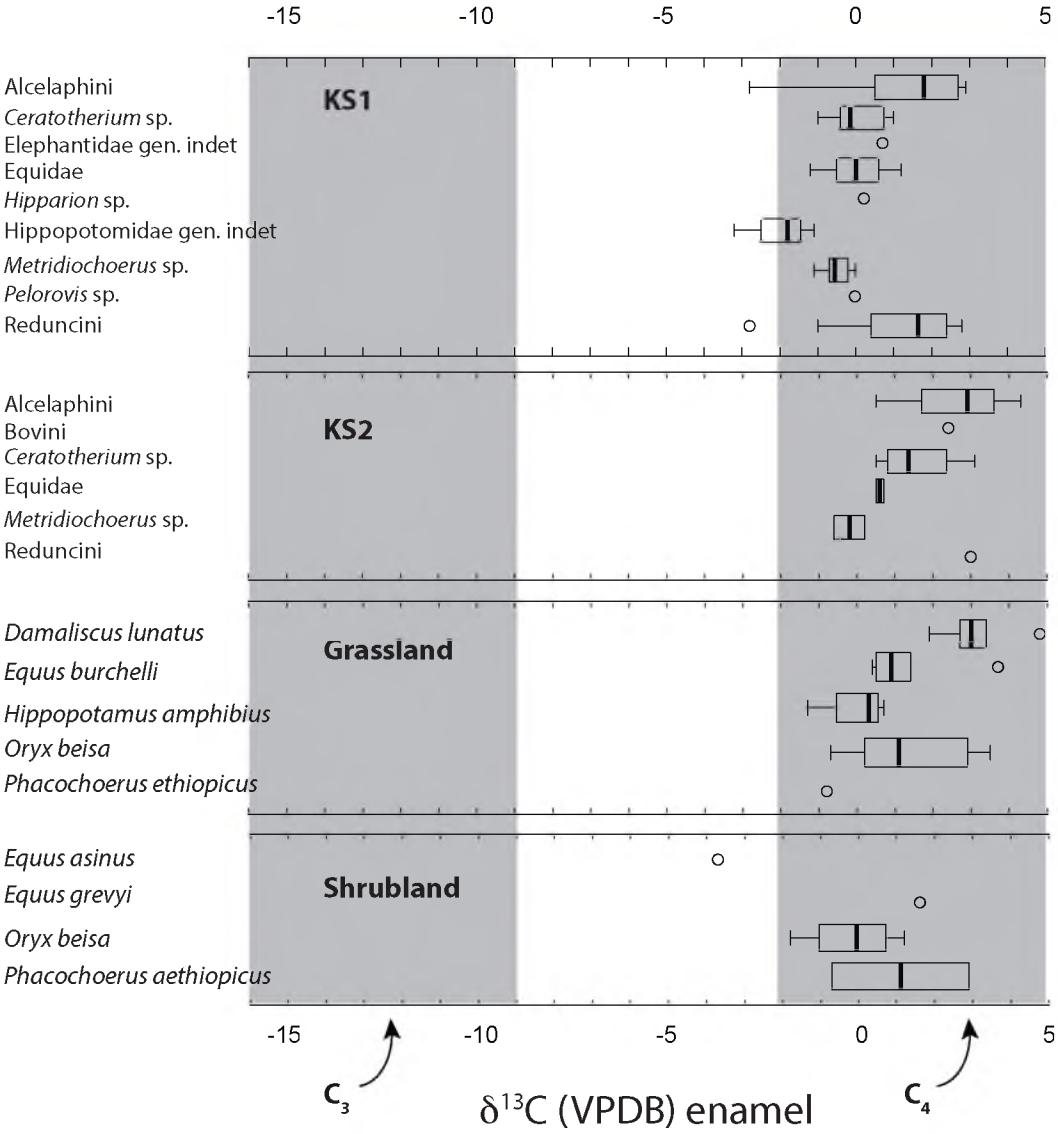

Figure 3 Box and whisker plot showing $\delta^{13}C$ values in ‰ for extant grazers and fossil enamel whose modern relatives are grazers. A vertical line within the box depicts median values, edges of boxes represent quartile values, whiskers indicate range, and outliers are plotted as circles.

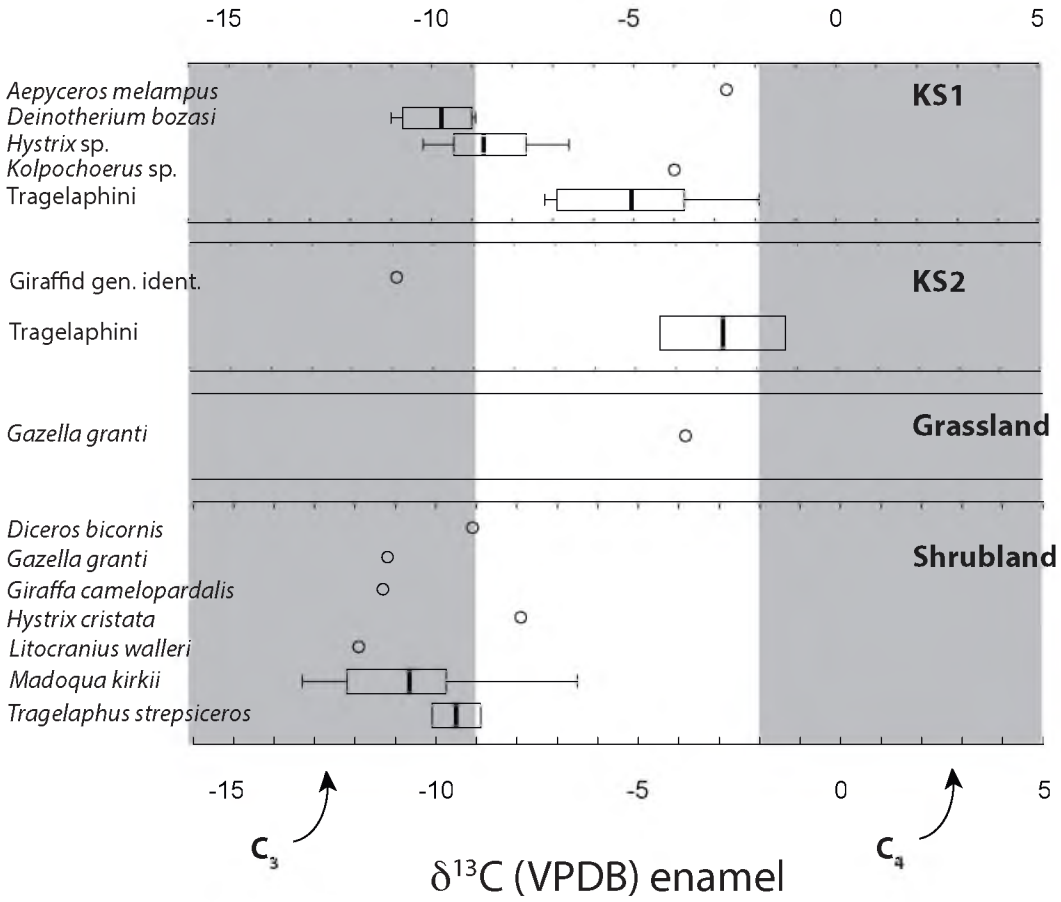

Figure 4 Box and whisker plot showing $\delta^{13}C$ values in ‰ for extant browsers and mixed feeders and fossil enamel whose modern relatives are browsers or mixed feeders, plotted in the same way as Figure 3.

Table 1 Average $\delta^{13}C$ and $\delta^{18}O$ enamel values (VPDB) for all taxa by Location. Standard deviation and number of samples are also listed.

Location	Mean $\delta^{13}C$ (‰)	σ	Mean $\delta^{18}O$ (‰)	σ		N
KS1	1.2	1.8	1.4	1.6	Alcelaphini	17
KS1	0		-0.5		Bovini	1
KS1	-9.9	1.0	-2.3	0.3	Deinothere	4
KS1	0.0	0.8	1.9	0.7	Equus	6
KS1	0.2		-1.8		Hipparion	1
KS1	-2.0	1.1	-1.2	1.9	Hippo	3
KS1	-8.5	1.8	-1.9	0.5	Hystrix	3
KS1	-2.7		0.4		Impala	1
KS1	-4		2.1		*K. limnetes*	1
KS1	-0.6	0.5	-0.3	1.7	*M. hopwoodi*	4
KS1	-0.3	0.1	2.5	0.4	*M. modestus*	2
KS1	0.7		-1.8		Proboscidean	1
KS1	1.1	1.8	1.0	1.3	Reduncini	10
KS1	0.1	0.7	-0.7	0.9	Rhino	8
KS1	-5.0	1.8	-0.4	1.1	Tragelaphini	16
KS2	2.6	1.9	0.8	1.1	Alcelaphini	3
KS2	2.4		-0.5		Bovini	1
KS2	0.6	0.1	1.9	1.4	Equidae	2
KS2	-10.9		0.4		Giraffe	1
KS2	-0.2	0.6	-0.1	1.0	*Metridiochoerus*	2
KS2	3		-0.9		Reduncini	1
KS2	1.6	1.1	0.3	0.7	Rhino	4
KS2	-2.9	2.2	0.7	0.4	Tragelaphini	2
Grassland	-3.8		10.5		Grant's Gazelle	1
Grassland	0	0.9	2.8	1.0	Hippo	4
Grassland	1.4	1.8	6.7	1.7	Oryx	5
Grassland	3.1	1.0	8.7	0.8	Topi	6
Grassland	-0.8		5.4		Warthog	1
Grassland	1.3	1.2	6.7	1.4	Zebra	6
Shrubland	-10.9		4.8		Baboon	1
Shrubland	-10.8	1.8	7.0	1.8	Dik-dik	16
Shrubland	-3.7		4.9		Donkey	1
Shrubland	-11.9		9.4		Gerenuk	1
Shrubland	-11.3		7.4		Giraffe	1
Shrubland	-11.2		8.6		Grant's Gazelle	1
Shrubland	1.6		9.9		Grevi's Zebra	1
Shrubland	-7.9		7.3		Hystrix	1
Shrubland	-9.5	0.8	12.4	1.8	Kudu	2
Shrubland	-0.2	1.3	5.6	1.1	Oryx	4
Shrubland	-9.1		2.3		Rhino	1
Shrubland	1.9	0.2	3.2	0.6	Warthog	2

The individuals represented by these modern biomes exhibit expected isotope values for their respective tribes (Cerling et al., 2003). Alcelaphines have been described as both obligate and variable grazers (Gagnon and Chew, 2000) but isotope studies show them to be the strictest of all African ungulate grazers. Beisa oryx are preferentially grazers (Kingdon, 2013); gerenuks are well-known browsers, rising up on their hindlegs to reach foliage (Kingdon and Pagel, 1997). Kirk's dik-dik is a dwarf antelope that consumes an almost wholly C_3 diet and is considered a hyperbrowser. They prefer dense shrub cover for food, shade, and protection (Kingdon, 2013).

While most Antilopini are categorized as browsers, Grant's gazelle has the widest range of $\delta^{13}C$ values found in extant Antilopini (Cerling et al., 2003). It will graze on grass that is young and green, but prefers herbs and shrub foliage, especially when other grass has been overgrazed (Kingdon and Pagel, 1997). Therefore, the discrepancy in $\delta^{13}C$ values between the grassland and shrubland gazelle is not surprising, especially considering the biomes in which they were found.

Fossil teeth of bovids at KS1 include representatives of the tribes Aepycerotini, Alcelaphini, Bovini, Reduncini, and Tragelaphini. Fossil teeth sampled from KS2 include representatives of the tribes Alcelaphini, Bovini, Reduncini, and Tragelaphini. Teeth sampled were mainly broken and whole molars and premolars. $\delta^{13}C_{enamel}$ values obtained were compared to modern values from Kenya and Uganda (Cerling et al., 2003) as well as the modern grassland and shrubland assemblages mentioned previously. Paleontological identifications beyond tribal level include *Aepyceros melampus* (impala), *Pelorovis, Kobus sigmoidalis/ellipsiprymnus* (waterbuck), and *Tragelaphus* (Brugal et al., 2003). No Hippotragini, Antilopini, or Madoquini are sampled from Kokiselei.

The single impala from KS1 has a $\delta^{13}C_{enamel}$ value of -2.7‰. In modern times, impala diet consists of a mix between grazing and browsing, but are not restricted to this average range and can take advantage of either C3 or C4 sources (Gagnon and Chew,

2000; Cerling et al., 2003; Copeland et al., 2009). A $\delta^{13}C$ value of -2.7‰ falls in this acceptable range.

Alcelaphines at KS1 display a wide range of $\delta^{13}C$ values, from -2.8‰ to +2.9‰ (average +1.2 ± 1.8‰, n=17). Alcelaphines at KS2 range from -2.0‰ to +4.3‰ (average +2.6 ± 1.9‰, n=3). These alcelaphines are depleted in ^{13}C in comparison to the modern grassland topi, but fall into the range measured by Cerling (2003).

Pelorovis has $\delta^{13}C$ values of -0.04‰ (n=1) and +2.4‰ (n=1) at KS1 and KS2, respectively. *Pelorovis,* an extinct genus of Bovini found in Africa from the late Pliocene into the early to mid-Pleistocene, is known for its large curved horns. It is considered a grazer, based on craniodental analysis (Mendoza et al., 2002; Martínez-Navarro et al., 2007). Extant Bovini are also grazers (Cerling et al., 2003).

Reduncines at KS1 include individuals of the genus *Kobus*, either *K. sigmoidalis*, or *K. ellpisiprymnus* (waterbuck). *K. sigmoidalis* is replaced by *K. ellpisiprymnus* in the Shungura Formation around 2.2 Ma but is found more recently in the Koobi Fora Formation. $\delta^{13}C$ values of reduncines at KS1 range from -2.8‰ to +2.8‰ (average +1.1 ± 1.8‰, n=10). These values are to be expected when compared to extant Reduncines, of which most are considered grazers, excluding the browsing Grey Rhebok (Cerling et al., 2003). Reduncini from KS2 have a $\delta^{13}C$ value of +3.0‰ (n=1).

Tragelaphines from KS1 display a range of $\delta^{13}C$ values from -1.9‰ to -7.2‰ (average -5.0 ± 1.8‰, n=16). Tragelaphines from KS2 have an average $\delta^{13}C$ value of -2.8 ± 2.1‰ (n=2). At both sites, these measured values are much higher than those measured for modern Tragelaphini. Cerling (2003) shows tragelaphines to be browsers and hyperbrowsers, with average $\delta^{13}C$ values that range from -10.6 ±1.3‰ to -16.7 ±1.1‰. Isotope studies of fossils show more variation in the diet of tragelaphines. There is isotopic evidence for a diet switch within members of Tragelaphini at 2.8 Ma in the

Shungura Formation at Turkana Basin, with more than a 4‰ increase from 3.2 Ma values (Bibi et al., 2012). Some studies in the Afar region of Ethiopia show similar C_4 input as far back as 4.6-4.2 Ma but a C_3 dominated diet similar to extant tragelaphines at 6.5-5.2 Ma (Levin et al., 2008) and 4.4 Ma (White et al., 2009). Although extant tragelaphines are considered browsers, grasses are eaten in the wet season or when green; some Tragelaphines, such as the common eland, are suggested to have a diet consisting of up to 60% C_4 (Gagnon and Chew, 2000). It appears that the diet of tragelaphines may depend on availability of vegetation and habitat use, explaining the wide variation.

Equidae

Modern Equidae from grassland are represented by a single species of zebra, *Equus quagga,* subspecies *burchelli*, also known as the common zebra. Measured enamel $\delta^{13}C$ values range from +0.4‰ to +3.7‰ (average +1.29 ± 1.2‰, n=6). Equidae sampled from shrubland includes both *Equus grevyi* (Grevy's zebra) and *Equus asinus* (donkey), with $\delta^{13}C$ values of +1.59‰ and -3.73‰, respectively. This value is expected for the zebra, but fairly negative for the donkey. $\delta^{13}C$ values between -8.0‰ and -2.0‰ are considered a mixed diet in equids (Ségalen et al., 2007), though values below -2.0‰ are not uncommon signals found in other ungulates considered as grazers or hypergrazers (Cerling et al., 2003). The donkey being domestic perhaps has had its selection limited by overgrazing. Its relative, the African Wild Ass, has been known to browse in addition to grazing (Kingdon, 2013).

Fossil teeth sampled from the family Equidae at KS1 include *Equus* and *Hipparion*. *Equus* ranges in $\delta^{13}C$ values from -1.2‰ to +1.2‰ (average -0.01 ± 0.89‰, n=6). The *Hipparion* has a $\delta^{13}C$ value of +0.2‰. Fossil teeth from KS2 included Equidae,

with an average $\delta^{13}C$ value of +0.6 ± 0.2‰ (n=2). Species level identification of equids can be difficult, so these are identified to genus level only. Studies of the evolution of rumen and cecal digestions as well as isotope studies show that equids are consistently grazers and switched to a C_4 diet as early as 9.9 Ma (Janis, 1976; Uno et al., 2011). The fossil isotope results reported here are slightly depleted in ^{13}C relative to the modern grassland equids, but are not outside the range measured by Cerling (2003) in grazing bovids.

Giraffidae

Modern giraffe from shrubland has a $\delta^{13}C$ value of -11.3‰ (n=1). Giraffes are widely acknowledged browsers and their diet records a primarily C_3 signal, as is evident by multiple studies (Leakey et al., 1996; Uno et al., 2011). Fossil enamel from giraffids at KS2 has a $\delta^{13}C$ value of -10.9‰ (n=1). These values are consistent with modern giraffid and other fossil giraffid diet (Levin et al., 2008).

Hippopotamidae

Modern grassland hippos display $\delta^{13}C$ values ranging from -1.26‰ to 0.72‰ (average +0.01 ± 0.9‰, n=4). No modern hippos were sampled from shrubland because hippos are rarely found there. Although traditionally considered grazers, recent carbon isotope studies contradict this accepted diet of the common hippo. A stable isotope study supports questions raised by Boisserie (2005), involving modern hippo enamel samples from Kenya, DR Congo, Uganda, and Tanzania. A total of 92 teeth from 75 individuals at these locations were analyzed. The average $\delta^{13}C$ value was -3.5 ± 2.4‰ and ranged from +1.5‰, a distinct grazer signal, all the way to -13.7‰ (Cerling et al., 2008). These values could be due to non-C_4 input or variation due to physiological fractionation.

Fossil hippo enamel at KS1 came from broken or fragmentary incisors. These hippos range in value from -3.2‰ to -1.1‰ (average -2.0 ± 1.1‰, n=3). Values are normal in comparison to extant and modern hippos.

Hystricidae

Analysis of a single Hystrix (porcupine) from modern shrubland yielded a $\delta^{13}C$ of -7.9‰ (n=1). No porcupines were analyzed from the modern grassland. Extant porcupines are generally mixed feeders, consuming roots, bulbs, bark, and have even been found to scavenge old animal remains (Kingdon and Pagel, 1997). Fossil enamel from the porcupines produce $\delta^{13}C$ values ranging from -10.2‰ to -6.6‰ (average -8.5 ± 1.8‰, n=3). Three genera are known from the Plio-Pleistocene—*Atherurus*, *Hystrix,* and the extinct *Xenohystrix* (Werdelin, 2010). Values for the fossil Hystrix exhibit a mixed C_3-C_4 diet, similar to the shrubland porcupines and literature descriptions.

Proboscidea

No modern Proboscidea are measured from the shrubland or grassland. Fossil proboscideans at KS1 include *Deinotherium* sp. and an unclassified proboscidean (Proboscidea gen. indet.). The measured range of $\delta^{13}C$ values for the deinotheres is -11.0‰ to -8.9‰ (average of -9.8 ± 1.0‰, n=4). The unclassified proboscidean has a $\delta^{13}C$ value of +1.1‰ (n=1). Deinotheres are an extinct group of the order Proboscidea separated from modern elephants at the family level; deinotheres had a C_3-dominated diet (Cerling et al., 1999). Measured values of fossil enamel for both deinotheres and the unidentified proboscidean are not surprising, and data from Cerling (1999) indicate that deinothere diet has been C_3-dominated from the early Miocene until the early Pleistocene. Aside from deinotheres, proboscideans had a C_4 dominated diet from 6 to 1 Ma, unlike their extant relatives, which range in $\delta^{13}C$ (diet) from -32‰ to -15‰.

Rhinocerotidae

No rhinos were measured from modern grassland. The rhino sampled from modern shrubland was identified as *Diceros bicornis* (black rhino). Measured $\delta^{13}C$ for the black rhino is -9.1‰ (n=1). Unlike the white rhino, black rhinos are browsers.

The fossil Rhinocerotidae enamel analyzed from Kokiselei consisted of enamel fragments and represented *Ceratotherium* sp. Commonly known as the white rhino, the extant *C. simum* subsists on a diet of grass. Fossil enamel sampled from white rhinos at KS1 have $\delta^{13}C$ values ranging from -1.0 to +1.0‰ (average +0.1 ± 1.0‰, n=8). At KS2 this $\delta^{13}C$ range is from +0.5‰ to +3.1‰, (average +1.6 ± 1.1‰, n=4). These $\delta^{13}C$ values are consistent with expected diet of the genus.

Suidae

Modern enamel was sampled from *Phacochoerus aethiopicus* (desert warthog) at both grassland and shrubland sites. The enamel from warthogs collected from grassland has a measured $\delta^{13}C$ value of -0.8‰ (n=1), whereas the enamel from shrubland warthogs has $\delta^{13}C$ values ranging from -2.3‰ to +2.0‰ (average +0.5 ± 2.4‰, n=3). Warthogs are primarily grazers, but will also dig for roots and rhyizomes (Kingdon and Pagel, 1997; Harris and Cerling, 2002).

The suid teeth sampled at KS1 and KS2 consist of broken molars and a single canine. Two extinct suid genera are present at KS1, *Kolpochoerus* and *Metridiochoerus*. The *Kolpochoerus* at KS1 has been identified to species level as *K. limnets (= K. heseloni)*. Two species of *Metridiochoerus* are known from KS1: *M. modestus* (n=2) and *M. hopwoodi* (n=4). The *Metridiochoerus* at KS2 have only been identified to genus level.

$\delta^{13}C$ values for suids range from -1.0 ± 1.4‰ (n=7) at KS1 to -0.2 ± 0.5‰ (n=2) at KS2. The largest varience in values is due to the *Kolpochoerus* at KS1, with a $\delta^{13}C$ value

of -4.0‰. *Kolpochoerus* is phylogenetically related to the modern suids *Potamochoerus* (modern bushpig and red river hog) and *Hylochoerus* (forest hog) (White and Harris, 1977). Some conflict exists in the literature as to the diet and habitat of *K. limnetes*. Dental microwear of *K. limnetes* is described as similar to that of *Potamochoerus*, an omnivorous suid, and skeletal classifications found a preference for closed habitats (Bishop et al., 2006). Conversely, stable isotope studies have shown *K. limnetes* to generally be grazing in nature, with an average $\delta^{13}C$ value of +0.5 ± 0.6‰ (n=8) (Harris and Cerling, 2002), though values as low as -6.3‰ have been reported (Bocherens et al., 1996). Bibi (2012) shows the same diet switch in *K. limnetes* as was seen in tragelaphines at ~2.8 Ma; a 2 to 6‰ shift is seen in $\delta^{13}C$ values between 3.2 and 2.8 Ma. Isotope values for *Kolpochoerus* prior to 3.2, between 4.6 and 4.2 Ma, are also indicative of a mixed C_3-C_4 diet (Levin et al., 2008). *Metridiochoerus* are also considered grazers, and have $\delta^{13}C$ values averaging +0.1 ± 0.3‰ (n=7) across various species of the genus (Harris and Cerling, 2002). The modern descendant of *Metridiochoerus* is *Phacochoerus*, which includes *P. aethiopicus* (desert warthog) and *P. africanus* (common warthog). The fossil isotope values of suids from Kokiselei are similar to the warthog values in both the shrubland and grassland, with the exception of *K. limnetes*.

Thryonomyidae

No modern Thryonomyidae enamel was analyzed, but some comparisons can be made to modern Thryonomyidae. Two extant species inhabit sub-Saharan Africa, *Thryonomys gregorianus* (savannah cane-rat) and *T. swinderianus* (marsh cane-rat). The former eats grass supplemented by fruits, bark, and roots while the latter eats mainly grass (Kingdon and Pagel, 1997). Fossil incisors from the cane rat were analyzed using laser ablation. $\delta^{13}C$ values for the cane rat range from -4.7‰ to -1.9‰ (average -3.1 ± 1.5‰, n=3). These are unidentified beyond family level and little is known about the

various species in the geologic record. Given the C_3 contribution to these measured results, and the lack of evidence for a marsh environment, the savannah cane-rat is probably the closer relative. These isotope values indicate a mixed diet dominated by C_4.

Paranthropus boisei

Two fossil teeth from *P. boisei* were analyzed from KS1. They had enamel $\delta^{13}C$ values of -1.3‰ and -2.4‰. These values are similar to other measured enamel for *P. boisei*, and indicate a C_4-dominated diet (Cerling et al., 2011).

Oxygen Isotopes and Moisture Conditions

Bovidae

Enamel measured from the modern environments exhibits a wide range of $\delta^{18}O$ values. In the grassland, the topi have $\delta^{18}O$ values ranging from +7.5‰ to +9.9‰ (average +8.7 ± 0.1‰, n=6) and the oryx range from +4.1‰ to +7.9‰ (average +6.7 ± 1.7‰, n=5). Grassland and shrubland Grant's gazelle have $\delta^{18}O$ values of +10.6‰ (n=1) and +8.6‰ (n=1), respectively. Shrubland gerenuk has a $\delta^{18}O$ value of +9.4‰ (n=1). The shrubland oryx range from +4.3‰ to +6.8‰ (average +5.6 ± 1.1‰, n=4), while the dik-diks range from +4.2‰ to +11.5‰ (average +7.0 ± 1.8‰, n=11) (Fig. 5).

Bovids are comprised of grazers and browsers, and include both EI and ES individuals. Based on diet, Alcelaphines, Aepycerotines, Hippotragines, and Reduncines could be considered EI while Antilopini, Madoquini, and Tragelaphines could be considered ES, but some physiological characteristics and behavioral patterns may influence their isotopic records (Kohn et al., 1996). Impala are water-dependent and live close to water. Topi are also water-dependent but can go without for months if consuming growing grass. The beisa oryx is fairly water-dependent but also efficient at water management and can sometimes get its water from succulent plants. Reduncines

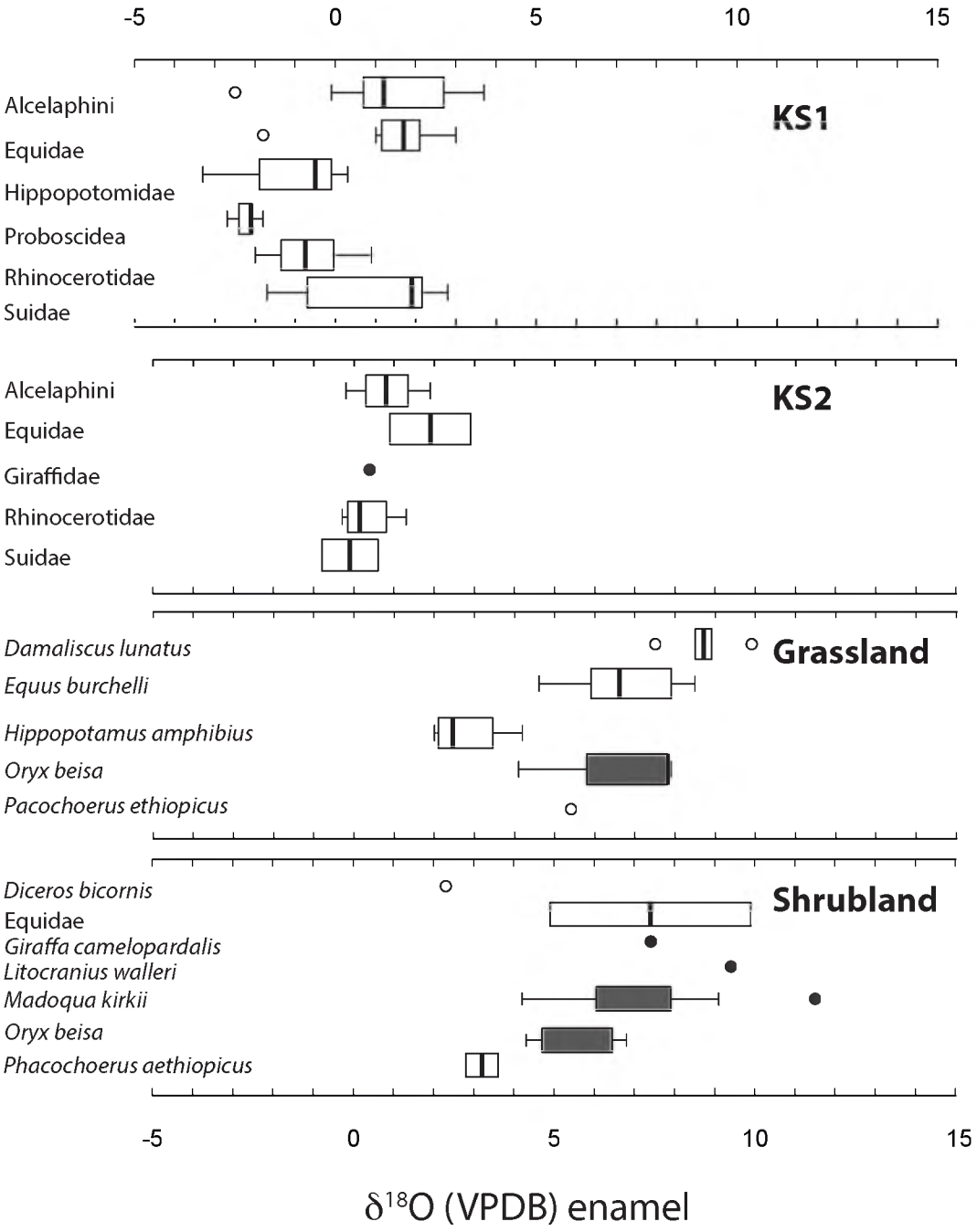

Figure 5 Box and whisker plot showing $\delta^{18}O$ values in ‰ for extant and fossil enamel, plotted in the same way as Figures 3 and 4. Evaporative insensitive (EI) taxa are represented by empty boxes, and evaporative sensitive (ES) taxa are represented by solid boxes and circles.

are mainly grazers, and so fairly water-dependent, but some species are less dependent, such as the mountain reedbuck (Kingdon and Pagel, 1997). Madoquini and Antilopini are browsers restricted to arid regions, and so their $\delta^{18}O$ signature is sensitive to evaporative enrichment. Water source for Tragelaphines varies between species. Some, like the lesser kudu, rarely drink, instead getting it through their food; others, like the mountain nyala, drink daily when available and prefer to be near a permanent water source (Kingdon, 2013). Previous research has established dik-diks and oryx as ES and topi as EI (Kohn et al., 1996; Levin et al., 2006).

The fossil enamel $\delta^{18}O$ value for the impala (Aepycerotini) in KS1 is +0.4‰. $\delta^{18}O$ values for Alcelaphini fossil enamel in KS1 range from -2.5‰ to +3.7‰ (average +1.5 ± 1.6‰, n=17). Alcelaphines from KS2 have $\delta^{18}O$ values that range from -0.2‰ to +1.9‰ (average +0.8 ± 1.1‰, n=3). Values for Bovini at KS1 and KS2 are -0.5‰ (n=1) and -0.5‰ (n=1), respectively. Reduncines from KS1 display an average $\delta^{18}O$ value of +1.0 ± 1.3‰ (n=10), ranging from -0.4‰ to +3.9‰. The reduncine from KS2 has a $\delta^{18}O$ value of -9.0‰ (n=1). Tragelaphine fossil enamel from KS1 have $\delta^{18}O$ values ranging from -0.4‰ to +3.9‰ (average +1.9 ± 1.3‰, n=16),. Tragelaphine fossil enamel from KS2 have $\delta^{18}O$ values ranging from +0.4‰ to +0.9‰ (average +0.7 ± 0.4‰, n=2) (Fig. 5).

Equidae

Common zebra from the modern grasslands have $\delta^{18}O$ values that range from +4.6‰ to +8.5‰ (average +6.7 ± 1.4‰, n=6). The zebra and donkey from the shrubland have $\delta^{18}O$ values of +9.9‰ and +5.0‰, respectively. Equids are water-dependent and therefore EI (Levin et al., 2006).

Fossil enamel from Kokiselei exhibit much lower $\delta^{18}O$ values. *Equus* in KS1 have $\delta^{18}O$ values ranging from +1.0‰ to +3.0‰ (average +1.9 ± 0.7‰, n=6). The hipparion

has a $\delta^{18}O$ value of -1.8‰ (n=1). At KS2, measured $\delta^{18}O$ values for Equids range from +0.9‰ to +2.9‰ (average +1.9 ± 1.4‰, n=2).

Giraffidae

Modern giraffes from the shrubland and from Koobi Fora have $\delta^{18}O$ values of +7.4‰ (n=1) and +3.6‰ (n=1), respectively. Fossil enamel from the giraffe at KS2 has a $\delta^{18}O$ value of +0.4‰ (n=1). As a browser, giraffes are considered ES and the oxygen signal in their diet tracks aridity. Research shows them to be the best species to be used for tracking this aridity (Levin et al., 2006). Based on this, the Kokiselei giraffe indicates an environment experiencing far less ^{18}O enrichment than the modern shrubland.

Hippopotamidae

Modern fossil hippo enamel from the grassland has $\delta^{18}O$ values ranging from +2.0‰ to +4.2‰ (average +2.8 ± 1.0‰, n=4). The hippos at Koobi Fora have $\delta^{18}O$ values ranging from -0.3‰ to +0.4‰ (average +0.2 ± 0.4‰, n=3). No shrubland hippos are known.

Fossil enamel from the hippos at KS1 produce $\delta^{18}O$ values that range from -3.3‰ to +0.3‰ (average -1.2 ± 1.9‰, n=3). Two hippos have values near -0.1‰ while a third hippo (-3.3‰) is the source of the high standard deviation.

Hippos are undeniably water-dependent, and the ideal EI species, but there can be variation. The cause of the differing values from enamel at KS1 can possibly be attributed to drinking source. River dwelling hippos have more negative $\delta^{18}O$ values than lake dwelling hippos (Cerling et al., 2008). Possibly the individual with the more negative $\delta^{18}O$ value lived in or near a river while the other two hippos lived in a lake, subject to evaporative enrichment.

Hystricidae

Modern shrubland hystrix has a $\delta^{18}O$ value of +7.3‰. Fossil enamel from the porcupines at KS1 have $\delta^{18}O$ values ranging from -2.4‰ to -1.5‰ (average -1.9 ± 0.5‰, n=3). Since porcupines take advantage of browsing resources, they could possibly be classified as ES. In one study, captive *H. cristata* were seen to drink regularly, but were not dependent on a constant source of water (Santini, 1980). No extensive research has determined their classification as either EI or ES.

Proboscidea

Proboscidea at KS1 includes deinothere and an unidentified Proboscidea. The deinotheres have $\delta^{18}O$ values ranging from -2.7‰ to -2.1‰ (average -2.3 ± 0.3‰, n=4). The proboscidean has a $\delta^{18}O$ value of -1.3‰ (n=1). Elephants are water-dependent and classified as EI (Levin et al., 2006).

Rhinocerotidae

Modern black rhinos from shrubland and from Koobi Fora have $\delta^{18}O$ values of +2.4‰ (n=1) and +0.1‰ (n=1), respectively. The rhinos from KS1 have $\delta^{18}O$ values that range from -2.0‰ to +0.9‰ (average -0.7 ± 1.0‰, n=8). The rhinos from KS2 range from -0.3‰ to +1.3‰ (average +0.3 ± 1.3‰, n=4). Both black and white rhinos are water-dependent, and so classified as EI (Levin et al., 2006).

Suidae

The modern grassland warthog has a $\delta^{18}O$ value of +5.4‰ (n=1); the modern shrubland warthogs have $\delta^{18}O$ values ranging from +2.8‰ to +4.3‰ (average +3.6 ± 0.7‰, n=3). Levin (2006) classifies the warthog as EI. Of the modern suids, warthogs

are less water-dependent than the bushpig and forest hog and are considered EI (Harris and Cerling, 2002; Levin et al., 2006). Stable isotope data indicate that *Metridiochoerus* is less water-dependent than *Kolpochoerus*.

Fossil enamel $\delta^{18}O$ values for the *M. hopwoodi* at KS1 range from -1.7‰ to +1.9‰ (average -0.3 ± 1.8‰, n=4). *M. modestus* $\delta^{18}O$ values average +2.5 ± 0.4‰ (n=2). The $\delta^{18}O$ value for the *K. limnetes* is +2.1‰ (n=1). Metridiochoerus at KS2 have an average $\delta^{18}O$ value of -0.1 ± 1.0‰ (n=1). The results presented here are inconsistent with the trend shown by Harris and Cerling (2002) and show *M. hopwoodi* as more water-dependent than *K. limnetes*. If these suids are grazers, though, they should all be fairly water-dependent.

Thryonomyidae

Thryonomyidae at Kokiselei were measured using laser ablation. This means that $\delta^{18}O$ values are measured from the carbonate and phosphate phase in the enamel, and are not viable for comparison. No modern cane rats were measured.

Paranthropus boisei

P. boisei from KS1 have $\delta^{18}O$ values of -2.9‰ and -3.7‰. These values are similar to the rest of the assemblage at KS1 and KS2 as well as other Pleistocene *P. boisei* in the literature (Cerling et al., 2011).

Community Structures

Modern

Having modern analogues of known biomes is beneficial for comparison to fossil sites. They can be used to understand how conditions at Lake Turkana 1.87 to 1.80 Ma compare to the modern environment.

Grassland

Samples from the grassland biome consist of 23 individuals from four sites. An average $\delta^{13}C$ value of +1.3 ± 2.0‰ indicates a C_4-dominated landscape. All taxa, including equids, bovids, suids, and hippopotamidae have C_4-dominated diets. Bovids comprise 52% of the sampled assemblage, with equids and hippos making up 26% and 17%, respectively. A single Grant's gazelle has the most negative $\delta^{13}C$ value (-3.8‰), but it does not fall outside of previous studies (Cerling et al., 2003) (Fig. 4).

An average $\delta^{18}O$ value of +6.6 ± 2.4‰ indicates waters that are more ^{18}O enriched than those of Kokiselei. A comparison between EI and ES species would include warthog, hippo, zebra, and topi as EI and oryx as ES. A $\delta^{18}O$ range of +2.8 ± 1.0‰ to +6.7 ± 1.7‰ between the hippo and oryx reflects the dry environment of modern Turkana (Fig. 5).

Shrubland

Samples from the shrubland biome consist of 34 individuals from seven sites. An average $\delta^{13}C$ value of -7.7 ± 4.9‰ suggests a mixed C_3/C_4-dominated landscape. Equids, suids, and some bovids have C_4-dominated diets. Rhinocerotidae, Giraffa, and most of the bovids have C_3-dominated diets. Dik-diks lend a heavy C_4 bias to the assemblage, comprising 47% of all individuals and 64% of the bovids; however, the kudu and Antilopini are also very C_3-dominated. Only the oryx have C_4-dominated diets. They

comprise 12% of the assemblage of samples from the shrubland. There is a marked separation between C_4- and C_3-dominated diets (Fig. 6).

$\delta^{18}O$ values are similar to those of the grassland, with an average value of +7.0 ± 2.8‰ indicating ^{18}O-enriched waters. EI species in the shrubland include warthog, black rhino, and zebras, while giraffe, gerenuk, dik dik, and oryx are ES. A $\delta^{18}O$ range of +4.6 ± 0.7‰ to +7.4‰ (n=1) between the warthog and giraffe is not a strong argument for high aridity, but it is likely that the EI individuals are sourcing their water from Lake Turkana (Fig. 5).

KS1

In the archaeological section of Kokiselei 1, a total of 80 enamel values were measured from a maximum of 80 individuals. It is possible that some teeth are from the same individuals. Average $\delta^{13}C$ enamel values of -1.6‰ ± 3.6 suggest a C_4-dominated landscape. Equids, suids, hippopotamids, and most bovids have C_4-dominated diets; tragelephines have mixed C_3/C_4-diets; Giraffa and Deinotherium have $\delta^{13}C$ values indicating a browsing diet. Bovids make up 56% of the individuals at KS1, with alcelaphines and reduncines making up 60% of those, and all the rest Tragelaphini but for the Bovini and impala. The next most common families of fauna are Rhinocerotidae and Suidae at 10% and 9%, respectively. Seventy percent of all $\delta^{13}C$ values are >-3.0‰. The oddities here are two taxa whose modern relatives are browsers, but at Kokiselei appear to be mixed feeders. Tragelaphines and *Kolpochoerus* are seen in KS1 to have a large C_4 component to their diet. The clear separation between C_3- and C_4-dominated diets seen in the modern shrubland is absent from KS1 (Fig. 6). Instead, the distinction is blurred. Including the switch from C_4 to C_3 that elephants underwent ~1Ma, there is good cause to consider a fundamental change occurring, either in the ecology of C_3 and C_4 plants or in behavioral and dietary preference within fauna.

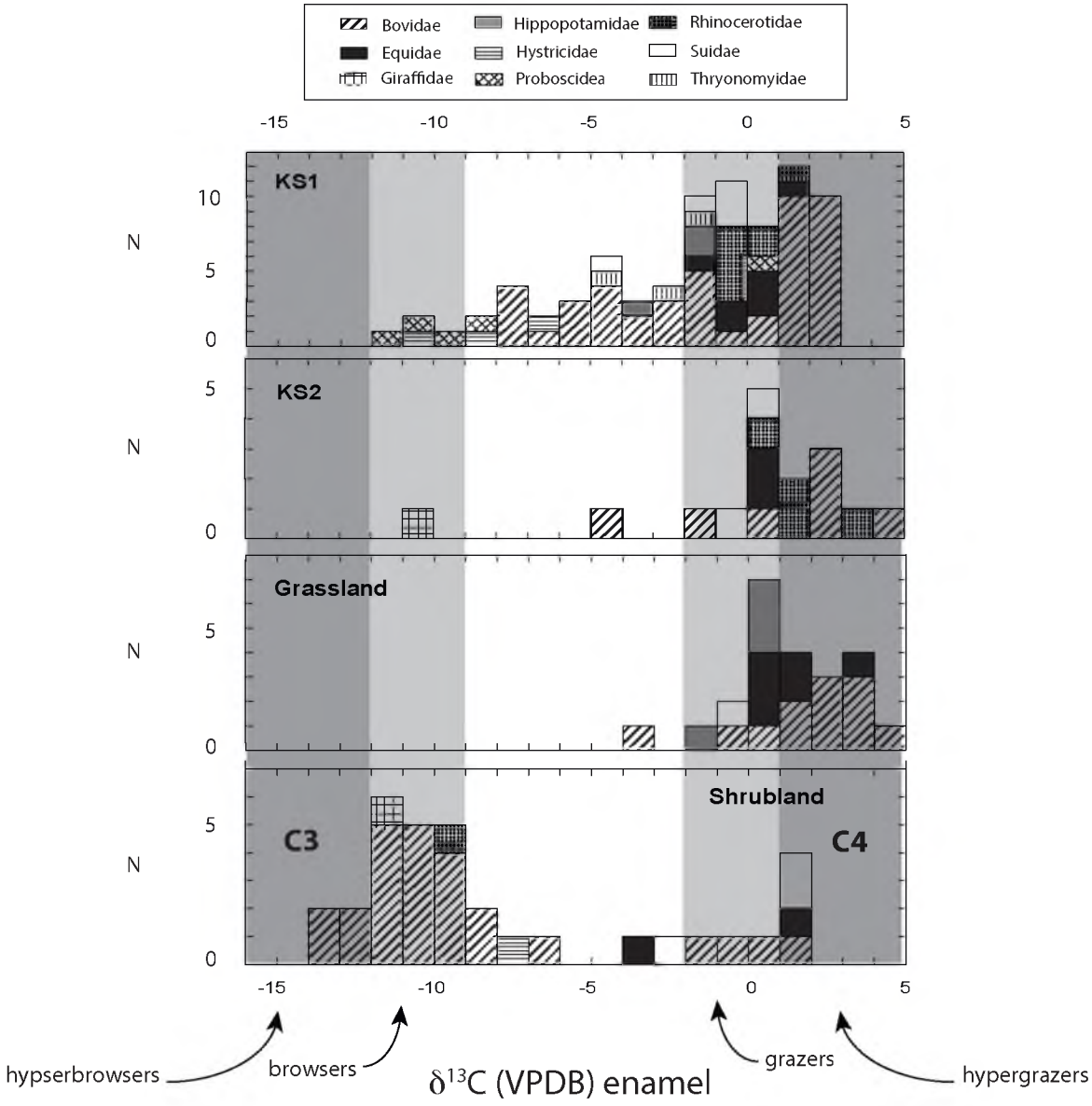

Figure 6 Histogram displaying range of $\delta^{13}C$ enamel values by site. A strict C_3 or C_4 diet is indicated by darker gray. A mixed C3-C4 diet falls in the unshaded region.

Average $\delta^{18}O$ values of +0.2 ± 1.7‰ indicate the presence of water relatively less enriched in ^{18}O than modern waters of the region (Fig. 5). This could be due to a strong fluvial presence, or an indication that Lake Lorenyang received significantly more recharge than modern Lake Turkana. The majority of this faunal assemblage is water-dependent and EI, their $\delta^{13}C$ values tracking local waters.

KS2

At Kokiselei 2, the average $\delta^{13}C$ value of -0.4 ± 4.5‰ (n=17) also suggests a C_4-dominated landscape. Equids, suids, rhinocerotids, and bovids have C_4-dominated diets; tragelaphines have mixed C_3/C_4-diets; *Giraffa* and *Deinotherium* have $\delta^{13}C$ values indicating a browsing diet. The average $\delta^{18}O$ value at KS2 is +0.5 ± 1.0‰, similar to KS1. Tragelaphines at KS2 show an even higher contribution of C_4 vegetation to their diet than at KS1 (Fig. 6).

In an attempt to look at WD ($\varepsilon_{ES\text{-}EI}$) enamel, $\delta^{18}O$ values are needed from both an ES and EI taxa. At KS2, $\varepsilon_{giraffe\text{-}rhino}$ could be used, but are not. Levin (2006) recommends $\varepsilon_{giraffe\text{-}hippo}$ over other ES/EI combinations and the use of 10 ES and 10 EI; results would be highly imprecise. As mention for KS1, an explanation for these low $\delta^{18}O$ values could be a relatively constant water source for the time, such as an open basin lake with significant recharge or the presence of a fluvial system; both possible as discussed in the geologic history of the basin. Alternatively, ES taxa have $\delta^{18}O$ values depleted in ^{18}O relative to ES taxa in the modern shrubland and grassland, making it highly probable that the basin in this area received far less evaporative enrichment.

CONCLUSIONS

Interest in describing the paleoclimate and paleoecology of East Africa is fueled by a desire to understand the environment under which hominins evolved and how it may have affected survival and diversification. Stable isotopes are common tools used in these fields to answer questions about vegetation, diet, and moisture conditions in the past. Carbon isotopic data from Kokiselei, Kenya show that *Paranthropus boisei* living in the Turkana Basin 1.87 to 1.80 Ma shared an ecosystem with fauna subsisting on mostly C_4 vegetation with some contribution of C_3, perhaps a wooded grassland environment. The majority of taxa from Kokiselei have C_4-dominated diets, indicating an abundance of grass in the early Pleistocene. Oxygen isotopic data show the habitat to have undergone less water stress than modern systems in this region, indicating a more mesic environment or the presence of significant fluvial input keeping ^{18}O enrichment low, or that animals were drinking dominantly from marginal streams. To solve this issue with more certainty, collection of more hippos and giraffes from this period and location would lead to more precise estimates of WD.

APPENDIX

DATA TABLES FOR ALL ENAMEL SAMPLES

Table A 1

$\delta^{13}C$ and $\delta^{18}O$ values for enamel from Kokiselei 1 (KS1) and Kokiselei 2 (KS2) in Kenya, East Africa

Sample ID	Taxon	$\delta^{13}C$ VPDB	$\delta^{18}O$ VPDB	Location	Tooth*	Collection Year
KS1-IV-O Aep	*Aepyceros melampus*	-2.7	0.4	KS1	m3	
KS1-III-N alc	Alcelaphini	-2.8	1.5	KS1	M	
KS1-P52-18	Alcelaphini	-1.1	0.4	KS1	M2	
KS1-P52-19	Alcelaphini	-1.7	0.7	KS1	M	
KS1-P52-5	Alcelaphini	-1.4	-0.1	KS1	M3	
KS1-G11	Alcelaphini	0.5	-2.5	KS1	m2	
KS1-H10	Alcelaphini	2.9	0.9	KS1	m2	1997
KS1-II	Alcelaphini	1.9	3.6	KS1	m2	1997
KS1-IV-E	Alcelaphini	2.7	0.7	KS1	m2	
KS1-IX Alc	Alcelaphini	1.5	3.7	KS1	P4	
KS1-M48	Alcelaphini	1.9	2.3	KS1	M	
KS1-N46	Alcelaphini	2.7	3.5	KS1	M	1987
KS1-N50	Alcelaphini	1.3	0.4	KS1	M2	
KS1-OSO	Alcelaphini	2.9	2.8	KS1	m2	1987
KS1-P48	Alcelaphini	1.8	2.7	KS1	m1	1987
KS1-P49	Alcelaphini	1.4	2.0	KS1	m2	
KS1-XIII.5	Alcelaphini	2.9	1.2	KS1	M2	
KS1-XIV Alc	Alcelaphini	2.7	0.8	KS1	m2	
KS1-N49	Bovini	0.0	-0.5	KS1	m2	1987
KS1-IX rhino	*Ceratotherium* sp.	-0.4	-1.3	KS1	fgt (p/m?)	
KS1-XIII N (1)	*Ceratotherium* sp.	0.9	-0.2	KS1	fgt (p/m?)	
KS1-XIII N (2)	*Ceratotherium* sp.	1.0	0.9	KS1	fgt (p/m?)	
KS1-XIII_S	*Ceratotherium* sp.	-0.1	-2.0	KS1	fgt (p/m?)	

Table A. 1 Continued

Sample ID	Taxon	$\delta^{13}C$ VPDB
KS1-XIII-N rhino	*Ceratotherium* sp.	0.6
KS1-XIX (1)	*Ceratotherium* sp.	-0.4
KS1-XIX (2)	*Ceratotherium* sp.	-0.2
KS1-XIX (3)	*Ceratotherium* sp.	-1.0
KS1-22	*Deinotherium bozasi*	-9.1
KS1-III-N (d)	*Deinotherium bozasi*	-11.0
KS1-IV (d)	*Deinotherium bozasi*	-8.9
KS1-IV-O (d)	*Deinotherium bozasi*	-10.4
KS1 N48 eq.	*Equus* sp.	-0.2
KS1-100	*Equus* sp.	-1.2
KS1 - 101 B	*Equus* sp.	1.2
KS1 102 eq.	*Equus* sp.	-0.5
KS1-O2	*Equus* sp.	0.6
KS1-O3	*Equus* sp.	0.2
KS1-XXII equid	*Hipparion* sp.	0.2
KS1-20.7.10	Hippopotomidae gen. indet.	-1.8
KS1-IX lg	Hippopotomidae gen. indet.	-1.1
KS1-IX sm	Hippopotomidae gen. indet.	-3.2
KS1-A51 hystr	*Hystrix* sp.	-6.6
KS1-east	*Hystrix* sp.	-10.2
KS1-XVIII (3)	*Hystrix* sp.	-8.7
KS1-24	*Kobus sigmoidalis/ellipsiprymnus*	2.5
KS1-A51 16 m1	*Kobus sigmoidalis/ellipsiprymnus*	1.5
KS1-A51 16 m3	*Kobus sigmoidalis/ellipsiprymnus*	2.4

$\delta^{18}O$ VPDB	Location	Tooth*	Collection Year
-0.4	KS1	fgt m	
-1.1	KS1	fgt (p/m?)	
-1.4	KS1	fgt (P/M?)	
0.1	KS1	fgt (p/m?)	
-2.7	KS1	fgt (p/m?)	1998
-2.1	KS1	fgt (p/m?)	
-2.1	KS1	fgt (p/m?)	
-2.4	KS1	fgt (p/m?)	
1.9	KS1		1987
1.0	KS1		
3.0	KS1	p2	
1.7	KS1		1987
1.3	KS1	i	
2.3	KS1	i	
-1.8	KS1	M	
0.3	KS1	i/c	2010
-0.5	KS1	i/c	1997
-3.3	KS1	fgt i/c	
-1.5	KS1		
-2.4	KS1		
-1.8	KS1		
0.1	KS1	M	
0.7	KS1	m1	1998
2.7	KS1	m3	1998

Table A. 1 Continued

Sample ID	Taxon	$\delta^{13}C$ VPDB
KS1-F49	*Kobus sigmoidalis/ellipsiprymnus*	-1.0
KS1-III_N (r)	*Kobus sigmoidalis/ellipsiprymnus*	1.2
KS1-IV red.	*Kobus sigmoidalis/ellipsiprymnus*	-2.8
KS1-M48	*Kobus sigmoidalis/ellipsiprymnus*	0.4
KS1-V	*Kobus sigmoidalis/ellipsiprymnus*	1.9
KS1-X_IX	*Kobus sigmoidalis/ellipsiprymnus*	2.8
KS1-ZA51-27	*Kobus sigmoidalis/ellipsiprymnus*	1.8
KS1-A51.3	*Kolpochoerus limnetes*	-4.0
KS1-163	*Metridiochoerus hopwoodi*	-0.7
KS1-R50 3	*Metridiochoerus hopwoodi*	-0.7
KS1-XIV suid	*Metridiochoerus hopwoodi*	0.0
KS1-XXIII	*Metridiochoerus hopwoodi*	-1.1
KS1-I11	*Metridiochoerus modestus*	-0.2
KS1-S49 17	*Metridiochoerus modestus*	-0.4
KNM WT 37749	*Paranthropus boisei*	-2.4
KNM 37750	*Paranthropus boisei*	-1.3
KS1-XVIII (light)	Proboscidea gen. indet.	1.1
KS1 23	*Thryonomys* sp.	-1.9
KS1 22	*Thryonomys* sp.	-4.7
KS1 Q46	*Thryonomys* sp.	-2.7
KS1-A49 trag.	*Tragelaphus* sp.	-3.3
KS1-F51	*Tragelaphus* sp.	-6.8
KS1-G11 trag	*Tragelaphus* sp.	-7.1
KS1-G11s (1) trag	*Tragelaphus* sp.	-5.3

$\delta^{18}O$ VPDB	Location	Tooth*	Collection Year
-0.4	KS1	m2	
0.9	KS1	m2	
0.4	KS1	m	1998
0.1	KS1	m2	1987
1.4	KS1	m2	1998
0.3	KS1	m3	
3.9	KS1	m2,m3	1998
2.1	KS1	m3	1998
-1.7	KS1	m3	
0.3	KS1	m3	
-1.7	KS1	m3	
1.9	KS1	m2	
2.2	KS1	m3	
2.8	KS1	m3	
-3.7	KS1	fgt m	
-2.9	KS1	fgt m	
-1.3	KS1	fgt (p/m?)	
	KS1		
	KS1		
	KS1		
-0.1	KS1		
0.9	KS1	P	
-1.3	KS1		
-1.7	KS1		1997

Table A. 1 Continued

Sample ID	Taxon	$\delta^{13}C$ VPDB
KS1-O49-26	*Tragelaphus* sp.	-4.2
KS1-VIII trag	*Tragelaphus* sp.	-7.1
KS1-VIII trag 2	*Tragelaphus* sp.	-1.9
KS1-1G-20	*Tragelaphus* sp.	-4.4
KS1-H10	*Tragelaphus* sp.	-5.4
KS1-H11	*Tragelaphus* sp.	-4.8
KS1-IV-O (trag)	*Tragelaphus* sp.	-5.5
KS1-Q50-23	*Tragelaphus* sp.	-2.1
KS1-XVIII trag	*Tragelaphus* sp.	-4.4
KS1-XXII	*Tragelaphus* sp.	-7.0
KS1-IX red.	*Tragelaphus* sp.	-3.3
KS1-XV	*Tragelaphus* sp.	-7.2
KS2-A 1	Alcelaphini	0.5
KS2-A6	Alcelaphini	4.3
KS2-O2 (A)	Alcelaphini	2.9
KS2-A10	*Ceratotherium* sp.	1.1
KS2-O2 C	*Ceratotherium* sp.	0.5
KS2-A 5	*Ceratotherium* sp.	1.6
KS2-A7	*Ceratotherium* sp.	3.1
KS2-O2 D	*Equus* sp.	0.7
KS2-A11	*Equus* sp.	0.5
KS2-gir surf	Giraffidae gen. indet.	-11.2
KS2-O2	Giraffidae gen. indet.	-10.9
KS2-A9	*Kobus* sp.	3.0

$\delta^{18}O$ VPDB	Location	Tooth*	Collection Year
0.0	KS1	m3	1987
0.8	KS1		
0.6	KS1		
-2.6	KS1		
-0.9	KS1		1997
-1.6	KS1		
-1.5	KS1		
0.8	KS1		
0.0	KS1		
0.3	KS1		
-0.5	KS1	m2	
0.4	KS1	m2	1998
-0.2	KS2		
0.8	KS2		
1.9	KS2		
0.0	KS2		
-0.3	KS2		
0.3	KS2		
1.3	KS2		
2.9	KS2		
0.9	KS2		
1.1	KS2		
0.4	KS2		
-0.9	KS2		

Table A. 1 Continued

Sample ID	Taxon	$\delta^{13}C$ VPDB	$\delta^{18}O$ VPDB	Location	Tooth*	Collection Year
KS2-A9	*Kobus* sp.	3.0	-0.9	KS2		
KS2-A 2	*Metridichoerus* sp.	-0.6	-0.8	KS2		
KS2-O2 B	*Metridichoerus* sp.	0.2	0.6	KS2		
KS1-EST	*Pelorovis* sp.	2.4	-0.5	KS2		
KS2-A 3	Tragelaphini	-1.3	0.4	KS2		
KS2-A8	Tragelaphini	-4.4	0.9	KS2		

Notes: VPDB refers to the isotopic standard Vienna Bee Dee Belemnite.

*Abbreviations for tooth position are as follows: r, right; l, left; m, molar; p, premolar, I, incisor; c, canine; d, deciduous.

Uppercase and lowercase letters refer to the maxillary and mandibular teeth, respectively. Fgt refers to fragment. If tooth is not listed, position is unknown.

Fossil samples collected by Jean-Philippe Brugal in 1980's and 90's, modern samples collected by Thure Cerling and $\delta^{13}C$ recorded as $\delta^{13}C_{1750}$

Table A. 2

Arid Shrubland assemblage

Sample ID	Taxon	$\delta^{13}C$ VPDB
TEC.K89.1	*Diceros bicornis*	-9.1
K99-065-Turk	*Equus asinus*	-3.7
20134	*Equus grevyi*	1.6
96 JW 13	*Gazella grantii*	-11.2
TEC.K89.3	*Giraffa camelopardalis*	-11.3
SU96:9	*Hystrix* sp.	-7.9
SU96:12	*Litocranius walleri*	-11.9
SU96:18	*Madoqua kirki*	-13.2
SU96:11	*Madoqua kirki*	-12.5
SU96:17	*Madoqua kirki*	-11.9
SU96:10	*Madoqua kirki*	-11.6
SU96:21	*Madoqua kirki*	-10.4
SU 3	*Madoqua kirki*	-13.3
SU-2-M2	*Madoqua kirki*	-10.9
SU 4 M2	*Madoqua kirki*	-8.8
K00-KF-320	*Madoqua kirki*	-12.5
85–KF-K00	*Madoqua kirki*	-11.2
K00-KF-316-M/3	*Madoqua kirki*	-10.4
K00-KF-319-M/3	*Madoqua kirki*	-9.8
96–KF-K00	*Madoqua kirki*	-9.8
K00-KF-317	*Madoqua kirki*	-9.7
86–KF-K00	*Madoqua kirki*	-9.5
K00-KF-318	*Madoqua kirki*	-6.5

$\delta^{18}O$ VPDB	Location	Tooth*	Collection Year
2.3	Koobi Fora	molar	1981
4.9	Turkana		1999
9.9	Koobi Fora	lP2	1974
8.6	Kanapoi	M3	1996
7.4	Tulu Bor river	molar	1974
7.3	Nabwal	M3	1996
9.4	Nabwal	M3	1996
6.0	Nabwal	mandible	1996
6.0	Nabwal	rM3	1996
6.7	Nabwal	mandible	1996
7.3	Nabwal	l & r M3	1996
9.1	Nabwal	M3	1996
8.8	Suregei	mandible	1995
6.2	Suregei	M2	1995
4.8	Suregei	M2	1995
4.2	Ileret	M	2000
7.1	Ileret	mandible	2000
6.1	Ileret	m3	2000
8.4	Ileret	M3	2000
6.4	Ileret	m3	2000
7.4	Ileret	m3	2000
11.5	Ileret	p3	2000
6.5	Ileret	mandible	2000

Table A. 2 Continued

Sample ID	Taxon	$\delta^{13}C$ VPDB
SU96:15	*Oryx beisa*	0.2
SU 6-M2	*Oryx beisa*	-1.8
SU-5-M3	*Oryx beisa*	-0.3
SU-5-M2	*Oryx beisa*	1.2
K00-KF-322	*Phacochoerus aethiopicus*	1.7
100–KF-K00	*Phacochoerus aethiopicus*	2.0
ET99-OMO-404	*Phacochoerus aethiopicus*	-2.3
SU96:14	*Tragelaphus strepsiceros*	-10.5
SU96:7	*Tragelaphus strepsiceros*	-10.1
SU96:23	*Tragelaphus strepsiceros*	-8.9

$\delta^{18}O$ VPDB	Location	Tooth*	Collection Year
6.8	Nabwal	mandible	1996
5.1	Suregei	M2	1995
4.3	Suregei	M3	1995
6.1	Suregei	M2	1995
2.8	Ileret	m3	2000
3.6	Ileret	m	2000
4.3			1999
14.1	Nabwal	mandible	1996
11.1	Nabwal	m3	1996
13.6	Nabwal	m3	1996

Table A. 3

Koobi Fora Grassland assemblage

Sample ID	Taxon	$\delta^{13}C$ VPDB	$\delta^{18}O$ VPDB
75–KF-K00	*Damaliscus lunatus*	4.8	7.5
TOPI-1 K.FORA	*Damaliscus lunatus*	1.9	8.9
K97-121-KF M2	*Damaliscus lunatus*	2.7	8.5
K97-120-KF M1	*Damaliscus lunatus*	2.7	8.8
K97-120-KF M2	*Damaliscus lunatus*	3.3	8.6
TOPI-3 K.FORA	*Damaliscus lunatus*	3.4	9.9
71–KF-K00	*Equus burchelli*	0.4	6.7
74–KF-K00	*Equus burchelli*	0.5	8.5
73–KF-K00	*Equus burchelli*	1.4	6.5
99–KF-K00	*Equus burchelli*	1.2	7.9
TEC.K89.6	*Equus burchelli*	0.6	4.6
47–KF-K00	*Equus burchelli*	3.7	5.9
G GAZELLE K.FORA	*Gazella granti*	-3.8	10.5
ET-161	*Hippopotamus amphibius*	-1.3	2.0
ET-162	*Hippopotamus amphibius*	0.2	2.2
TEC.K89.2	*Hippopotamus amphibius*	0.4	2.7
OM-6102B	*Hippopotamus amphibus*	0.7	4.2
72–KF-K00	*Oryx beisa*	3.5	7.8
ORYX-1 K.FORA	*Oryx beisa*	-0.7	7.8
ORYX-2 K.FORA	*Oryx beisa*	2.9	7.9
TEC-K89.9E	*Oryx beisa*	0.2	5.8
OM 1530	*Oryx beisa*	1.1	4.1
TEC.K89.5	*Phacochoerus ethiopicus*	-0.8	5.4

Location	Tooth*	Collection Year
Area 102		2000
Koobi Fora		1999
Koobi Fora	M2	1997
Koobi Fora	M1	1997
Koobi Fora	M2	1997
Koobi Fora		1999
Area 102	m2	2000
Area 102	dec. incisor	2000
Area 102	m3	2000
Ileret	m3	2000
Koobi Fora	molar	1974
		2000
Koobi Fora		1999
Koobi Fora	M	1971
Koobi Fora	molar	1990
Koobi Fora	molar	1974
Lake Turkana	lm4	1975
Area 102	M3	2000
Koobi Fora		1999
Koobi Fora		1999
Koobi Fora	molar	1974
Lake Turkana	RM2	1968
Koobi Fora		1974

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